Oxygen levels in mound nests of *Crocodylus porosus* and *Alligator mississippiensis* are high, and gas exchange occurs primarily by diffusion, not convection

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ABSTRACT

We measured gas exchange of eggs and mound material as well as gas concentrations at different times during incubation in the mound nests of the salt water crocodile, *Crocodylus porosus* and the American alligator, *Alligator mississippiensis*. Oxygen consumption increased gradually during development in both species, peaking well before hatching (at approximately 80% of the incubation period in *A. mississippiensis*). The RE of eggs at 30 °C and at peak O_2 was 0.74 in *C. porosus* and 0.70 in *A. mississippiensis*. In a typical mound nest of *C. porosus*, the oxygen demand of the decomposing nest itself is likely to be 4-7 times that of the clutch at the end of incubation, with a respiratory exchange ratio (RE) of about 0.9. Despite the oxygen demand of nest material, the gaseous environment of the nest is favourable for embryonic development. The lowest pO_2 we measured was 125 Torr in nests of *C. porosus* and 133 Torr in nests of *A. mississippiensis*, with maximum pCO_2 of 22 Torr for *C. porosus* and 23 Torr for *A. mississippiensis*. Although convective gas exchange might be expected through the nest mound, gas exchange between the clutch and the outside air occurs by diffusion. No unifying theory has yet emerged to provide a satisfactory explanation for the apparently random distribution of hole-nesting and mound-nesting within the Crocodylidae.

Key words: crocodilian, incubation, eggs, oxygen consumption, carbon dioxide production, respiratory exchange ratio

Introduction

Crocodilians are distinctly dimorphic in their nesting habits (Greer 1971). Some species excavate a nest cavity in the substratum, usually in sand (hole-nesters). Others build a conspicuous mound composed of the adjacent substratum, vegetation and litter, or sometimes vegetation alone (particularly certain grasses) and lay their eggs in a cavity dug within it (mound-nesters) (Greer 1970, 1971, Webb *et al.* 1983, Ferguson 1985).

While hole-nesting and mound-nesting both promote buffered temperature and humidity for the developing embryos (Chabreck 1973, Magnusson 1979, Ferguson and Joanen 1982, Lutz and Dunbar-Cooper 1984, Ferguson 1985), neither habit would seem to be advantageous for gas exchange. The limited rate of diffusion of gases through soil surrounding underground nests of reptiles and birds (particularly sea turtles and mound-building Megapode birds) results in O_2 tensions that are lower, and CO_2 tensions that are higher than atmospheric, which may limit clutch sizes in reptiles and birds (Seymour and Ackerman 1980). Nevertheless, pO_2 and pCO_2 in hole nests dug in soil by freshwater turtles, *Chelodina expansa*, show concentrations that are unlikely to compromise development, except after heavy rain (Booth 1998). Additionally, O_2 tensions in hole nests dug in beach sand by leatherback turtles, *Dermochelys coriacea*, remain close to atmospheric until the second half of incubation when, just before hatching, the lowest values (to 120 Torr) are unlikely to pose a threat (Wallace *et al.* 2004). Few studies have been made of crocodilian nests. Gas tensions in two hole nests of the American crocodile, *Crocodylus acutus*, dug in a sand/shell substrate, were not severe throughout incubation, with pO_2 falling to about 130 Torr and pCO2 rising to 16 Torr (Lutz and Dunbar-Cooper 1984). In a third *C. acutus* nest, dug into sand/shell, pO_2 fell to 116 Torr about two thirds of the way through incubation and then rose again. Incomplete data for other nests, in marl, also showed pO_2 in the range of 120-140 Torr and pCO_2 of 13-20 Torr, but an infertile clutch and a nest that was killed by flooding had CO_2 tension rising to 64 Torr and O_2 tension falling to 84 Torr, probably the consequence of bacterial activity. Overall, the data are too variable to make generalisations about gas tensions in nests of *C. acutus*, except to say that in successful nests gas tensions are favourable, and that the type of substratum in which the nest hole is dug may have an important influence. O_2 tensions in nests of the hole-nesting *C. johnstoni* fall by 17.9 ± 12.0 Torr (n=9) during incubation, while CO_2 tensions rise by 16.3 ±

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13.5 Torr, the lowest O_2 tensions (e.g. 102 Torr) occurring in association with heavy rainstorms (Whitehead 1987). Thus, hole-nesting in a sandy or friable clay substratum is not associated with particularly inimical gas tensions. It might be expected that the oxygen consumption associated with decomposition creates a very different situation in mound nests. However, in the only example studied so far, O_2 and CO_2 tensions in mounds of *Alligator mississippiensis* although variable over the last half of incubation, averaged about 140 Torr and 16 Torr respectively (Booth and Thompson 1991).

Nesting mounds of *C. porosus* and *A. mississippiensis* may be l m or more high and 1.5-2.0 m across and are constructed of vegetation (particularly certain grasses) mixed with mud or other soil, shell grit, sticks, or vines depending upon what is available (McIlhenny 1935, Webb *et al.* 1977). The high component of organic matter in the mound is in striking contrast to the situation in hole-nesting crocodilians and one might suspect that its decomposition would provide a low oxygen environment. We tested this hypothesis by measuring gas tensions in the mound nests in both *C. porosus* and *A. mississippiensis*.

Material and methods

The study of *C. porosus* was conducted near Maningrida, Northern Territory on natural nests along the Liverpool or Tomkinson Rivers and at the Edward River Crocodile Farm, Pormpuraaw, Queensland. Laboratory analyses were conducted either on site or in the School of Biological Sciences, The University of Sydney or in the Zoology Department, The University of Queensland. The study of *A. mississippiensis* nests was conducted at Paynes Prairie, Alachua County, Florida. Analyses were carried out in the Zoology Department of the University of Florida on the day of sampling.

Nest Gases.

(a) *Crocodylus porosus*: Nest gases were sampled from twenty-one *C. porosus* nests, constructed from a diversity of materials (Table 1).

Of the nine “wild” nests of *C. porosus*, the Myeeli Swamp (12°05’14”S 134°10’00” E) nest site was located on foot by Laurence Taplin and Janet Taylor in March 1980, following advice from local aborigines; the eight Tomkinson River nests were located by aerial survey from a Cessna 206

Table 1. Nest gases in a series of natural nests of ***Crocodylus porosus***, some with eggs and some without.

Nest identifier or date	Nest material	Age of eggs	pO_2 Torr	pCO_2 Torr
(a) Myeeli Swamp, Liverpool River, near Maningrida N.T.				
17 March 1981	Grass, soil	80+ days	148	4.1
18 March 1981			146	5.7
19 March 1981			144	6.7
20 March 1981			145	5.3
21 March 1981			147	4.4
(b) Edward River Crocodile Farm, Pormpuraaw, Qld. 12 march 1982				
A	Grass, shellgrit	Removed	144	12.5
B	Shellgrit, soil	Removed	135	21.2
C	Sticks, leaves, shellgrit	Removed	148	<7.5
D	Sand,soil, shellgrit	Removed	142	14.3
E	Leaves, sticks, shellgrit	Removed	135	17.2
F	Grass. Mud	Removed	138	16.0
G	Grass	Removed	146	10.0
H	Grass, shellgrit	Removed	146	8.3
I	Grass	Removed	145	9.5
J	Grass	Removed	145	8.0
K	Soil, shellgrit, grass	Removed	142	11.0
L	Sand, shellgrit	Removed	134	20.0
(c) Tomkinson River, near Maningrida, N.T. 3 April 1982				
2	Grass, soil	Empty	146	<7.5
3	Soil, vines	Infertile	145	7.5
4	Grass	12 days	146	<7.5
5	Vines. Soil	12 days	128	16.0
6	Vines, soil	38 days	142	9.1
7	Grass, soil	38 days	145	<7.5
8	Grass, soil	56 days	136	15.0
9	Soil, sticks	75 days	130	22.0

aircraft on March 27, 1982, using the method described by Magnusson *et al.* (1978). After location from the air (Figure 1), nests were visited by boat, examined and gas samples taken (Figure 2). Of the eight Tomkinson nests, six had fertile eggs at various stages, one had infertile eggs and one lacked eggs. At the Edward River Crocodile Farm, the breeding adults are fenced within a large (14 ha) natural area which includes a complex lagoon in which breeding occurs naturally. Eggs are removed from nests to incubators within a couple of days of laying, so all the nests we examined there were empty.

The Myeeli Swamp nest (Figures 3, 4) was sampled repetitively. A small diameter sampling tube, sealed with a Luer-Lok tap, was inserted into the nest four days before sampling commenced, its tip situated deep within the clutch, and the nest material replaced carefully. Samples of gases were removed from all other nests of *C. porosus* using a simple probe made by taping a similar thin tube to a brass rod. The probe was inserted into nests as far as the clutch and, after clearing the dead-space, samples were taken into greased 20 mL glass syringes and sealed with a metal cap. Analyses for pO_2 and pCO_2 were made using a Radiometer PHM-71, (or PHM-73) and BMS-3 Gas Analyser calibrated with standard gas mixes and with reference to a mercury barometer (laboratory) or an aircraft altimeter set to airfield elevation (field) to determine barometric pressure. Up to 14 days elapsed between sample collection in the Northern Territory and analysis in Sydney. However, comparison between “end expired” breath samples from Grigg, taken and stored at the same time as the nest gases and fresh samples taken at the time of analysis showed no difference, confirming the reliability of using greased glass syringes for sample storage and transport.

(b) *Alligator mississippiensis*: Ten nests of *A. mississippiensis* were located on levee banks at Paynes Prairie, Alachua County, Florida, in August, 1988 (Figures 5, 6). A small hole was made in the side of each nest to expose the egg chamber. Some eggs were removed carefully from the edge of each clutch to allow insertion of a gas sampling tube and thermocouple wire to the centre of the clutch. The eggs were then replaced into their exact positions, with egg orientations being maintained throughout the procedure and nest material replaced to close the excavation hole. A second tube and thermocouple was located in each nest at the same depth as the eggs, but some distance from the clutch. Tygon catheter tubing (I.D. = 0.8 mm, O.D. = 2.4mm) was used to sample gases and 38 S.W.G. copper-constantan thermocouple wire and a Comark Thermocouple reader were used to measure temperature (Figure 5). A 3 ml syringe barrel was attached to the end of the tubing in the nests with a 20 gauge needle to provide a dead space for gas sampling. A 20 gauge needle was fitted to the free end outside of the

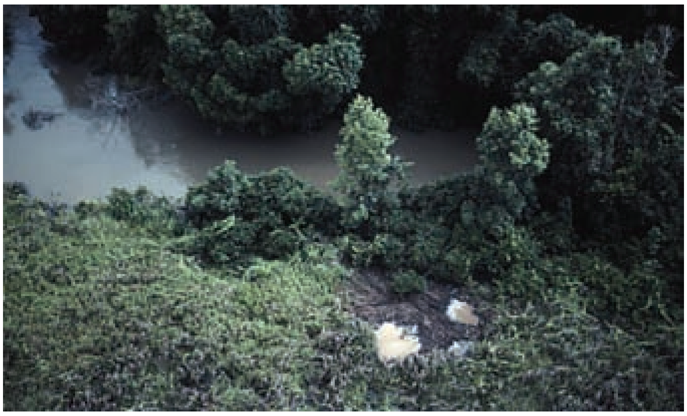

Figure 1. Aerial view of *C. porosus* nest, Cadell River, February 1980. Photo, G. Grigg.

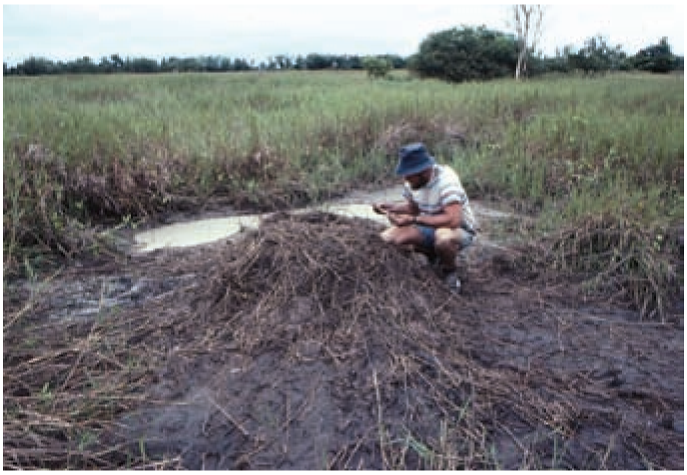

Figure 2. Grass and mud nest of *C. porosus* with wallow behind. Liverpool River NT, March 1982. Photo, G. Vorlicek

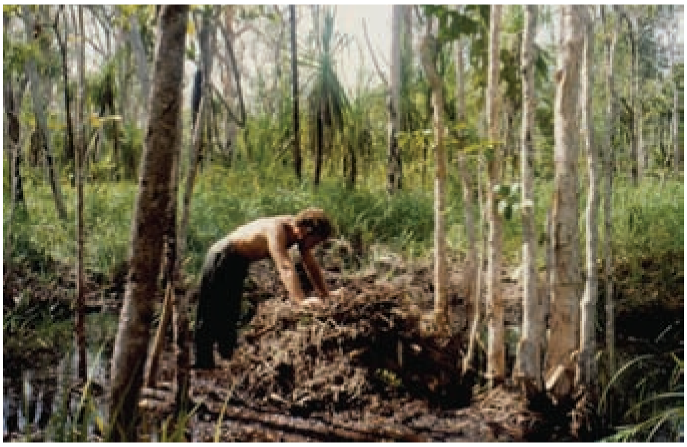

Figure 3. David Kirshner examines the grass nest of *C. porosus* in Myeeli Swamp, a paperbark swamp draining into the Liverpool River N.T. Note the wallow, left of picture. Photo, P. Harlow.

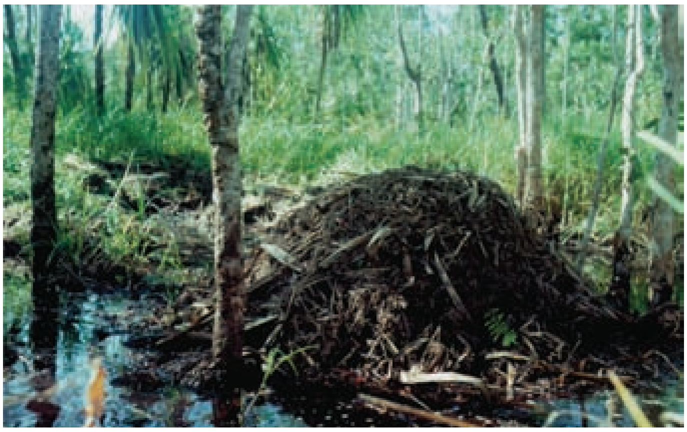

Figure 4. The grass nest of *C. porosus* in Myeeli Swamp. Photo, P. Harlow.

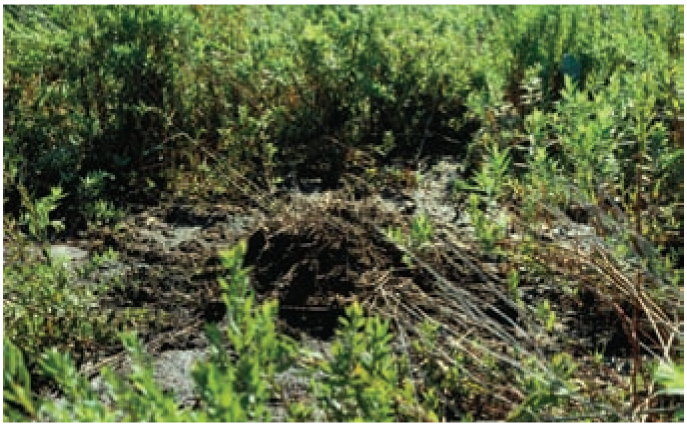

Figure 5. Grass nest of *Alligator mississippiensis* on Paynes Prairie, near Gainesville, Florida. The nest was fitted with thermocouple wire for measuring temperature and a tube for sampling gases. Note the wallow in the background and the thermocouple reader. Photo, M. Thompson.

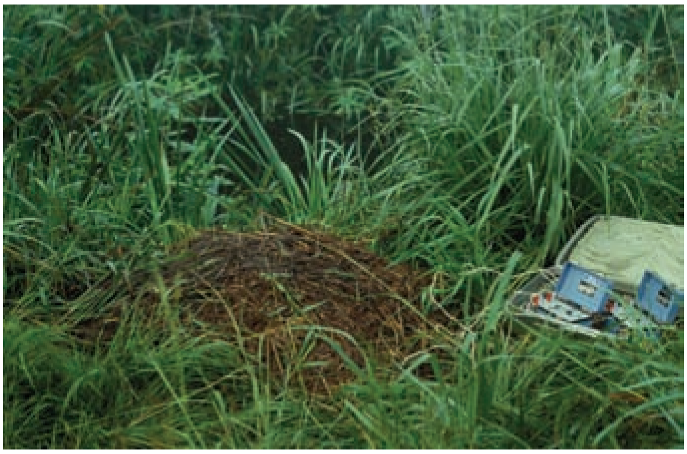

Figure 6. Another grass nest of *A. mississippiensis* on Paynes Prairie, Alachua County, near Gainesville, Florida. Photo. M. Thompson. Note the similarity of the nests of *A. mississippiensis* to those of *C. porosus*. Photo. M. Thompson.

mound to enable gas samples to be taken into a 60 ml plastic syringe. This needle was plugged between measurements with a plastic stopper. Seven nests were "wired" on 1st , two on the 10th and one on 15th August, 1988.

Gas samples were taken and temperatures measured at 2-4 day intervals during the last half of incubation. Samples were taken before 10.00 a.m. and returned to the laboratory immediately. At least twice the dead space in the tubing was expelled through a three-way stopcock before a sample was collected into the syringe. Sample analysis was completed before 1500 h in the Zoology Department of the University of Florida on the day of sampling. The time from collection of the first sample to analysis of the last was usually less than 6 h. A test of the diffusion of the plastic syringes to O_2 and CO_2 over similar partial pressure gradients to that found in the nests showed little (pCO_2) or no (pPO_2) change over 6-10 h. pO2 was measured in an Ametek S3A-2 oxygen analyser and $pC0_2$ in an Ametek CD-3A CO2 analyser calibrated with 7% CO2. Percentage gas concentrations were converted to partial pressures using barometric pressure measured for that day at University of Florida and pH_2O of saturated air at the temperature measured in the nest.

Unfortunately, only two of the nests of *A. mississippiensis* survived predation until hatching. Data were recorded in clutches until destroyed by predators and some nests without eggs were monitored for a short time with no eggs.

Oxygen consumption, RE of eggs and nesting material and determination of organic content of nesting material

(a) *Crocodylus porosus*

Nesting material: 40-60 g samples of nesting material were taken at depths of 100-200 mm from nests of *C. porosus* chosen randomly at Edward River. Aerated samples were transferred to glass jars with lids incorporating two plastic Luer-Lok taps. The vessels were then sealed and placed in the dark in a constant temperature room at 31°C, mimicking natural conditions in a nest. Air was sampled from the vessels a day later and analysed immediately for pO_2 and pCO_2 as described above for *C. porosus* nest gases. Oxygen consumption and pCO_2 production were calculated with reference to the volume of airspace in the vessel at the completion of the measurement period, determined by filling each vessel, still containing the nest material, with water. Organic content of each sample was determined by comparing oven-dried weight with weight after 4 h exposure to 450 °C in a muffle furnace.

Two *C. porosus* nests at Edward River, a large one and a small one, were weighed sack full by sack full, using a clockface balance.

Eggs: Rates of O_2 consumption and CO_2 production of eggs of *C. porosus* at different ages were determined at Edward River Crocodile Farm, using eggs that had been removed from nests immediately after laying and held in a large incubator at approximately 30 °C. Measurements were made in the same type of simple respirometry vessel as the nest material, following similar general methodology. Eggs from 12 nests were used and ages were known within a couple of days. To determine the effects of temperature on oxygen consumption and respiratory exchange ratio (RE), measurements were made at three temperatures, using the same methodology. This was carried out at Maningrida on full term eggs taken from a large nest in Myeeli Swamp .

(b) *Alligator mississippiensis*

Eggs: Two clutches of eggs of *A. mississippiensis* were collected at Orange Lake, Alachua County on 21 July, 1988. Six eggs from each clutch were incubated at 30 ˚C half buried in vermiculite at approximately -730 kPa (based on calibration for the vermiculite prepared using a Wesor 33-T microvoltmeter and C-52 sample chamber). On the basis of the egg bands, one clutch was estimated to be 21 days old and the other 31-32 days (Mason, pers. comm.). Each clutch was incubated in a separate container. Rates of O_2 consumption and CO_2 production were measured at least twice per week using closed system respirometry as described by Thompson (1989), until the eggs hatched.

Data are presented as mean ± one standard deviation.

Results

Counter-intuitively, oxygen tensions within nests were consistently high in nests of both species; none was lower than 128 Torr in *C. porosus* and 133 Torr in *A. mississippiensis* and values were usually much higher. The highest tension of carbon dioxide was 22 Torr in *C. porosus* and 23 Torr in *A. mississippiensis*, but was typically much lower (Table 1, Figure 7).

Rate of oxygen consumption ($\dot{V}O_2$) of *C. porosus* nest material ranged from 3-26 ml.kg^{-1}.h^{-1} and there is a curvilinear relationship between $\dot{V}O_2$ and the amount of organic matter in the nest material, a lower percentage of organic matter showing lower oxygen consumption (Figure 8). The two nests of *C. porosus* weighed at Edward River were 112 and 68 kg. The maximum oxygen requirement of nests of this size is thus 2,912 ml.h^{-1} and

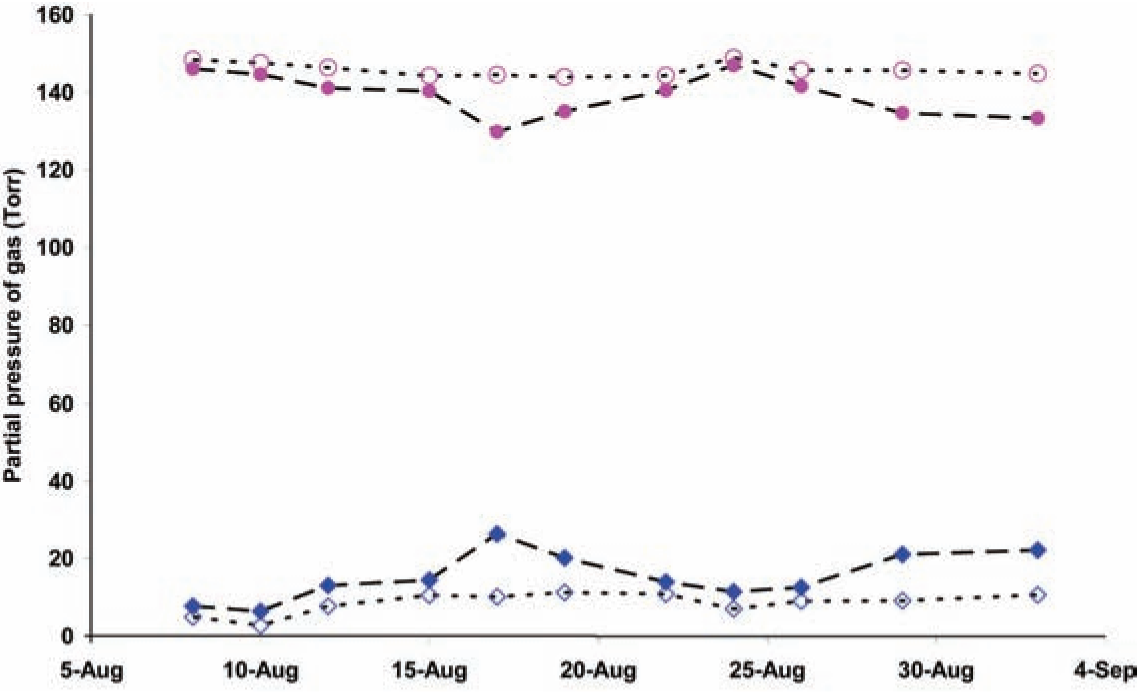

Figure 7. O_2 (pink circles) and CO_2 (blue diamonds) tensions measured in nests of *A. mississippiensis* throughout the last half of incubation. Solid symbols represent gas tensions within the clutch of eggs and open symbols, within the mound material away from the egg chamber of nests with eggs.

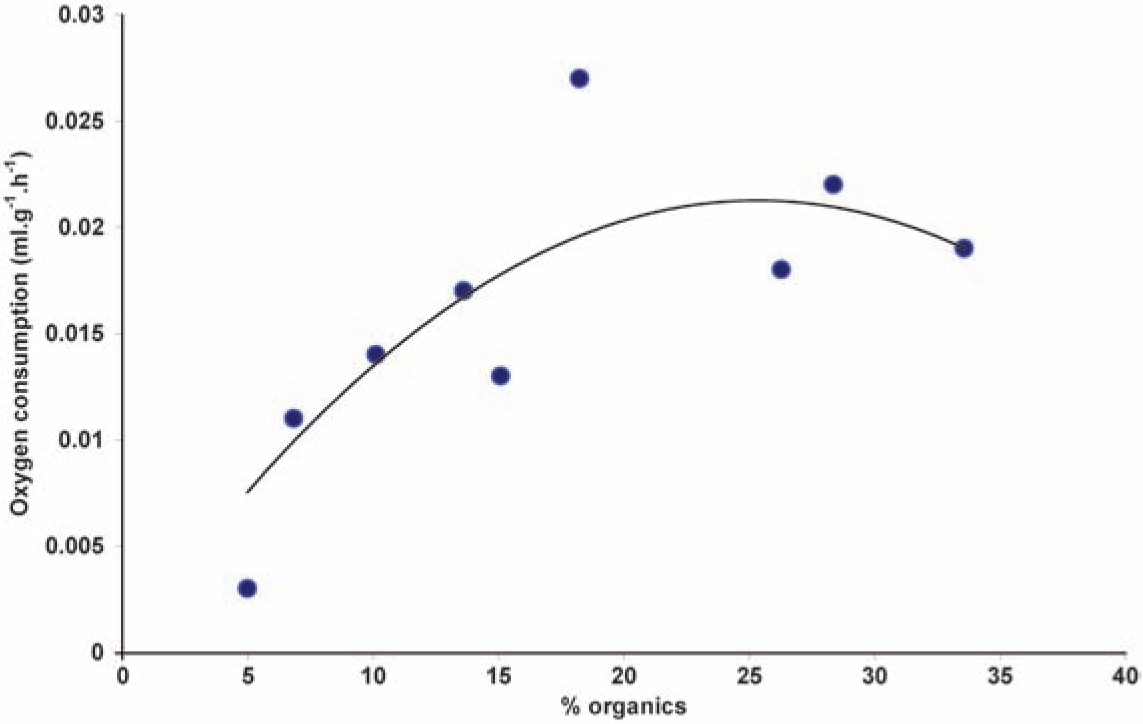

Figure 8. Rate of oxygen consumption of nest material (ml.g^{-1}.h^{-1}) as a function of the percent organic matter in nests of *C. porosus*.

1,768 ml.h^{-1}. RE for a variety of nesting materials ranged from 0.80 to 0.95 (0.885 ± 0.047) (Table 2). Thus, maximum rates of CO_2 production for nests of 112 and 68 kg are 2,766 ml.h^{-1} and 1,680 ml.h^{-1}.

$\dot{V}O_2$ of eggs of both *C. porosus* and *A. mississippiensis* rise during incubation, reach a peak about 80% of the way through incubation and then fall (Figures 9,10). The maximum $\dot{V}O_2$ measured for 120 g eggs of

Table 2. Oxygen consumption ($\dot{V}0_2$), respiratory exchange ratio (RE) and percentage organic matter of nest material in a series of nests of *C. porosus*.

Nest #	Nest Material	V02 (ml.g^{-1}.h^{-1})	RE	Organic matter (% of wet mass)	
11	Soil,shellgrit	0.0034	0.895	5.9	5.0
12	Grass,shellgrit	0.0135	0.950	15.4	15.1
13	Grass	0.0187	0.927	36.3	33.9
14	Grass	0.0216	0.805	31.1	28.4
15	Grass	0.0143	0.880	11.6	10.2
16	Grass	0.0183	0.870	26.9	26.4
17	Grass	0.0167	0.880	14.4	13.7
18	Grass	0.0273	0.930	18.7	18.4
19	Soil, shellgrit	0.0105	0.83	7.9	6.8
Mean		0.0160	0.89		
S.D.		0.0068	0.047		

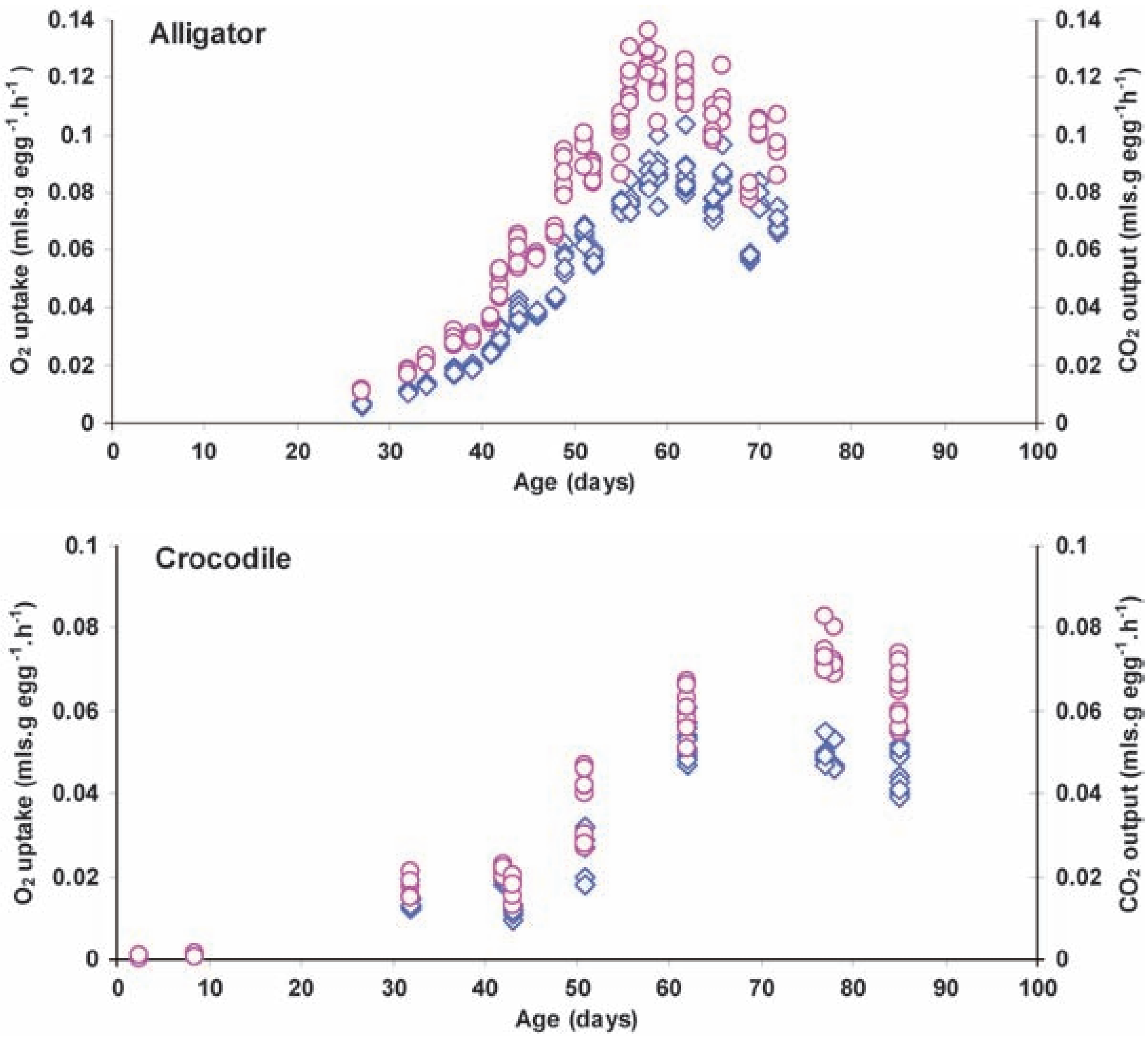

Figure 9. Rates of oxygen consumption (pink circles) and carbon dioxide production (blue diamonds) in eggs of *A. mississippiensis* and *C. porosus*. All measurements were made at 30 °C..

C. porosus at 30 °C was 0.074 ±0.005 ml.g $egg^{-1}.h^{-1}$, and 0.127 ± 0.008 ml.g $egg^{-1}.h^{-1}$ for *A. mississippiensis*. The RE of *C. porosus* eggs at the peak of oxygen consumption was 0.74 at 30 °C (Figure 9) and 0.70 for *A. mississippiensis*.

The $\dot{V}O_2$ and $\dot{V}CO_2$ of eggs of *C. porosus* rose with temperature between 25°C and 35 °C (Figure 10). Q_{10} was 2.1 below 30 °C, but there was an indication of a down-regulation of metabolism (Q_{10} = 1.62) between 30 °C and 35 °C, in the range of temperatures normally encountered during incubation (farms usually choose 32 °C).

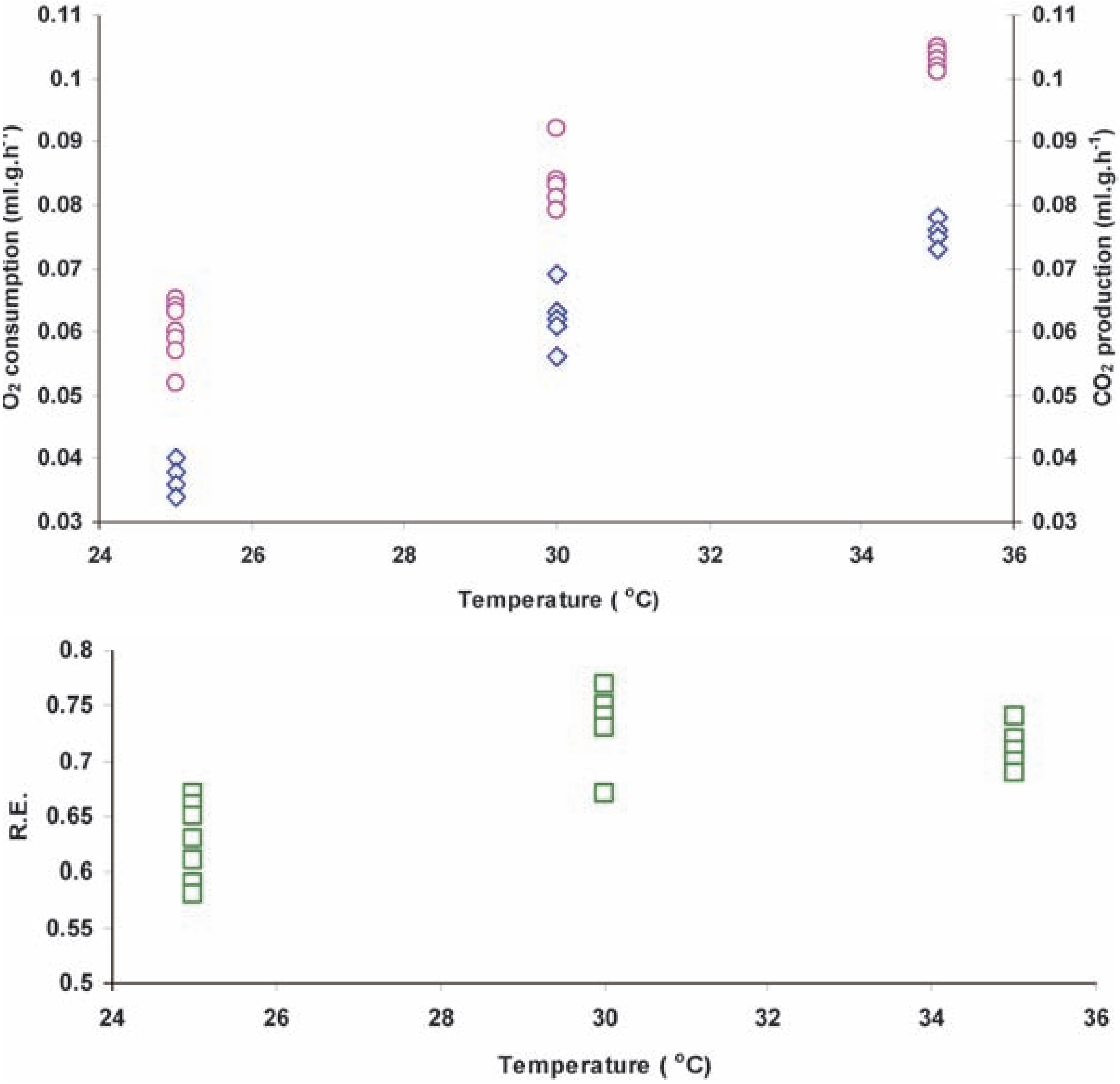

Figure 10. Oxygen consumption (pink circles), carbon dioxide production (blue diamonds) and R.E. (lower panel) of full term eggs of *C. porosus* at three different temperatures.

Discussion

The similar range of O_2 and CO_2 tensions in nests with and without eggs (Table 1) confirmed the expectation that, unlike in hole-nesters, the metabolism of mound material has a major influence on internal gas tensions, as it does in mound nests of megapode birds (Seymour et al., 1986). To compare total oxygen requirements, relative weights and rates of oxygen consumption of both clutch and mound must be taken into consideration. An average clutch of *C. porosus* comprises fifty 113 g eggs, a total of 5.65 kg, and of *A. mississippiensis*, 38.9 x 84 g eggs, a total of 3.27 kg (Ferguson 1985), so the clutch mass is far outweighed by the mass of the mound. Further, the total oxygen requirement (1,768-2,912 ml.h^{-1}) of the mound material therefore exceeds that of the clutch throughout incubation, even at the pre-hatch peak of 700 ml.h^{-1} for a clutch of *C. porosus* eggs and 415 ml.h^{-1} for *A. mississippiensis*. The role of the oxygen consumption of the mound material in dictating the gaseous environment in which the eggs develop sets mound-builders apart from the hole-nesting *C. acutus* (Lutz and Dunbar-Cooper 1984), *C. johnstoni* (Whitehead 1987) and sea turtles (Ackerman 1977), in which the clutch is surrounded by sand, shell grit or other inorganic matter that has low oxygen consumption and where oxygen tensions fall progressively throughout development as a consequence of egg respiration.

Minimum O_2 tensions of 125 Torr are unlikely to restrict the oxygen demand of the eggs. Furthermore, embryonic metabolism is not inhibited by CO_2 to 30 Torr in *C. porosus* (Grigg and Beard, unpublished data), so CO_2 tensions of 22 Torr should not be detrimental. The gaseous environment of mound nests is therefore unlikely to be unfavourable for embryonic development.

The observation of such high partial pressures of oxygen within mounds of decomposing organic matter throughout incubation prompts questions about whether gas exchange with the atmosphere may occur by convection rather than by diffusion. The question can be resolved by plotting a pCO_2/pO_2 diagram (Wangensteen and Rahn 1970/71). The slope of the pCO_2/pO_2 line should reflect the mechanism/s by which gas exchange occurs between the egg-mound and the atmosphere (Seymour *et al.* 1986). The possible mechanisms are diffusion and convection, or a combination of both. Similar analyses in hole nests of sea turtles (Ackerman 1977) and mound-building birds (Seymour *et al.* 1986) showed convincingly that the relative changes in pO_2 and pCO_2 within the clutch may be described by a steady-state diffusion model. In those cases, the data fell along pCO_2/pO_2 lines with slopes of -0.90 and -0.96, as would be predicted for the RE of turtle eggs and avian eggs (0.7) according to the diffusion equation of Wangensteen and Rahn (1970/71):

$$pCO_2 = \frac{\underline{RE\ (\Delta\ pO_2)}}{0.78} \qquad (1)$$

(where 0.78 is the ratio of the rate of CO_2 to O_2 diffusion in air and ΔpO_2 is the difference between pO_2 inside and outside of the nest).

The equation which describes convective gas exchange is:

$$pCO_2 = RE\ (\Delta pO_2) \qquad (2)$$

(Wangensteen and Rahn 1970/71).

With these two equations, plus knowledge about the RE of nesting material and the relative contributions of nest material and the clutch, one can calculate whether gas exchange in the mound nests of *C. porosus* occurs by diffusion, convection or a combination of both.

Using the diffusion and convection equations above, predicted pCO_2/pO2 lines at REs of 0.88 and 0.74 can be generated for diffusion and convection models respectively (Figure 11). Bearing in mind the range of measured REs of nesting material, a diffusion model is adequate to explain gas exchange in an empty nest. It is noteworthy that points deriving from nests with eggs fell along a line with lesser slope, as would be predicted by the lower "combined RE" of mound plus eggs. This is more difficult to model because the combined RE changes as development proceeds but, in any event, exchange by

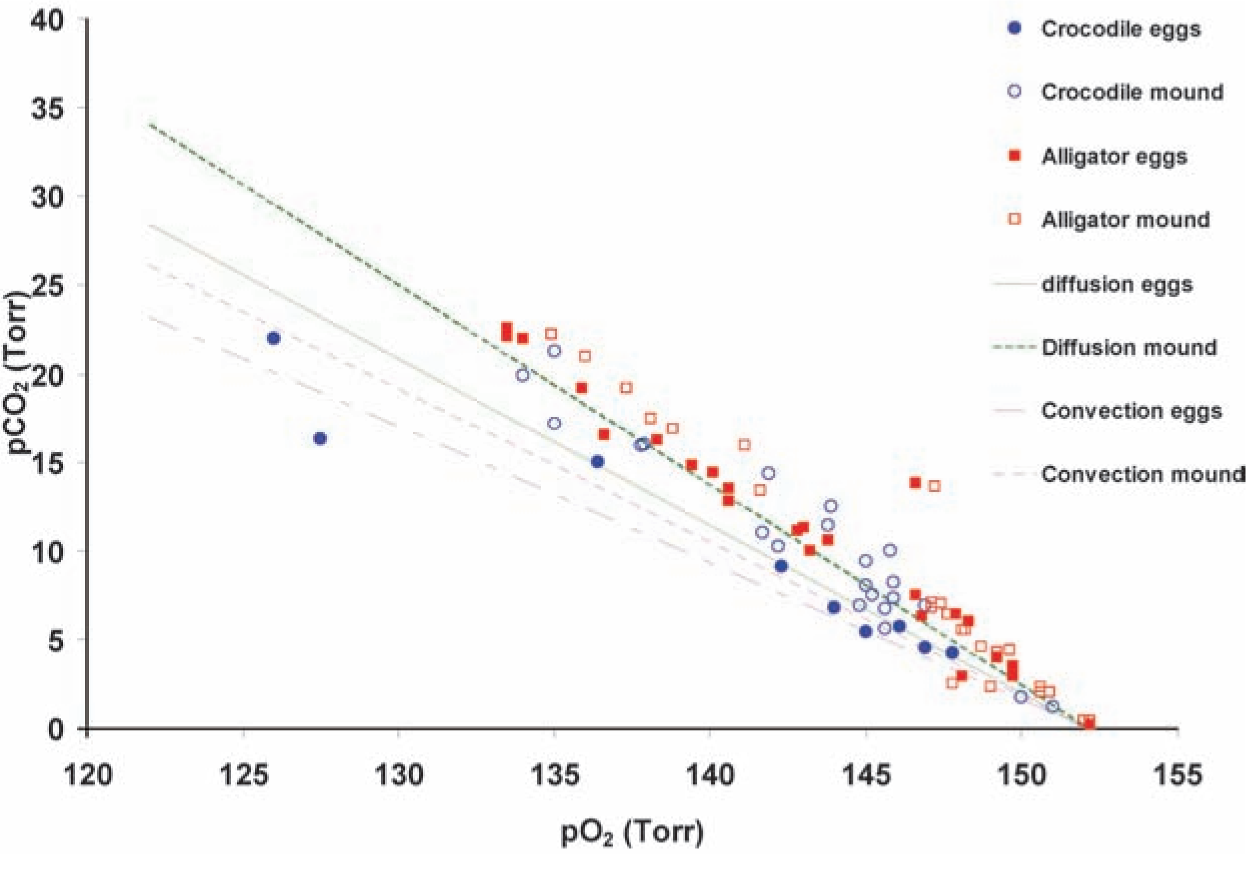

Figure 11. A pO2/pCO2 curve for diffusive (green) and conductive (pink) gas exchange calculated for REs of 0.883 to represent respiration in the nest and 0.74 to represent the eggs. The points represent individual measurements from nests of *C. porosus* (blue circles) and *A. mississippiensis* (red squares) both with (filled symbols) and without (open symbols) eggs.

diffusion is adequate to explain the points derived from nests with eggs, too. Thus, rates of CO_2 accumulation are higher in relation to oxygen consumed than would be expected if convection were significant.

Comparison with data from hole-nesting marine reptiles is illuminating. At the end of incubation in *Caretta caretta* and *Chelonia mydas* clutches, which consume oxygen at 300-400 ml.h^{-1} in a medium (sand) with negligible oxygen consumption, oxygen tensions fall to 80-100 Torr ($pC0_2$ = 30-40 Torr) at the end of incubation (Ackerman 1977). At the end of incubation in the (predominantly grass) Myeeli Swamp nest, with fifty 120 g eggs, clutch oxygen consumption can be calculated at about 750 ml.h^{-1}, in a medium with an oxygen consumption, per unit weight, of about 20% that of a full term clutch, yet oxygen tensions remained about 145 Torr (pCO_2 4-7 Torr) in that nest.

If diffusion is the mechanism of gas exchange in both hole and mound nests, how is it that the vegetation mounds of *C. porosus* and *A. mississippiensis* apparently provide a more beneficial oxygen and carbon dioxide environment than the hole nests of sea turtles (and, by implication, of hole-nesting crocodiles) in sand? Two factors are likely to be of importance, the larger surface area of a mound compared to a hole-nest and the diffusion resistance of mound material which is likely to be considerably less than that of sand.

These considerations are relevant to any discussion about the occurrence of mound-nesting or hole-nesting habits among the various crocodilian species. Greer (1970) addressed this question in relation to crocodilian phylogeny and concluded that hole nesting is primitive. However, views on crocodilian phylogeny have changed dramatically since 1970, especially in light of the work of Llew Densmore and Chris Brochu (see Densmore and Owen 1989, White and Densmore 2000, Brochu 2000, Brochu 2003). Specifically, while fossils of both crocodile and alligator lineages are known since the upper Cretaceous (Taplin and Grigg 1989), the extant members of *Crocodylus* are thought to have radiated within the last 5 million years. Six out of twelve *Crocodylus* species nest in holes, including *C. acutus* which may sometimes use a mound (Campbell 1972), yet none of the alligators or caimans is a hole-nester. *Osteolaemus* (Crocodylidae) uses a mound, as does *Tomistoma* (Gavialidae), but *Gavialis gangeticus* (Gavialidae) nests in a hole. Greer's hypothesis that hole-nesting is primitive is not supported, and any explanation for the adoption of one or other nesting habit is more likely to be found by looking among ecological than phylogenetic correlates. Whether in holes or mounds, successful crocodilian nests provide protection and an appropriate temperature and hydric environment for the developing embryos. We have shown that mound-nesting is not disadvantageous from an oxygen-supply point of view, and may even be advantageous. More data and a thorough review of the nesting biology across the Crocodylia may lead to the emergence of a satisfactory explanation for what now looks like a random distribution of the mound-nesting habit among Gavialidae and Crocodylidae.

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